BURROWING ACTIVITIES OF *PERIPLOMA MARGARITACEUM* (LAMARCK, 1801) (BIVALVIA: ANOMALODESMATA: PERIPLOMATIDAE)

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ABSTRACT

Observations made on *Periploma margaritaceum*, from the Indian River, Florida, show that it uses its siphons as a bellows to cleanse the mantle cavity of sand and debris that enters during burrowing activities. Measurements of specimens of this hermaphroditic species from collections made throughout 1982 indicate that recruitment from spring spawning occurs during the fall. The species inhabits silty sand in shallow water and burrows into the substratum to a depth of a few centimeters. Fundamental differences exist between Periplomatidae and Laternulidae that involve anatomy and function of the siphons, and orientation of the animals in the substratum.

The Periplomatidae, a small family of marine bivalves, are world-wide in distribution (Rosewater, 1968). The valves are thin, fragile and have an intrinsic fracture through the umbos that proceeds ventrally for some distance and is buttressed with shelly material on the inner surface of the valves. Hinges are simple and no conventional teeth are present, their function being taken over by a spoon shaped chondrophore in either valve. A lithodesma usually extends transversely, from one valve to the other, behind the chondrophore. A ligament fits into a depression in each chondrophore further connecting the valves. The thin shell apparently does not offer much protection from predators, some populations showing a high degree of predation (Rosewater, 1980). *Periploma* apparently evidences “r-selection” and manages to exist as a biological entity through the production of sufficient numbers of young to replace those lost by predation or the natural death of aging populations (see discussion in Vermeij, 1978, pp. 170–173). The latter is an assumption, however, and little is known of the natural history and biology of most of these bivalves. This is because they are infaunal and when removed from their habitat are very shy and cryptic in behavior (Morse, 1919). Pelseneer (1911) gave one of the first reports on the anatomy of a periplomatid, describing *Periploma ovata* ? [sic], which was said to possess separate siphons, the excurrent being larger. Allen (1958, 1960) studied the anatomy and behavior of *Cochlodesma praetenue* (Pulteney, 1799) which he found buried in the substratum usually with the right side down, the incurrent siphon extending toward the surface, and the excurrent siphon directed posteriorly. Morton (1981a) summarized information concerning the subclass Anomalodesmata and proposed that families Thraciidae, Laternulidae, and Periplomatidae comprise the superfamily Thraciacea Stoliczka, 1870. Morton (1981b) extensively examined the biology and anatomy of another species of periplomatid, *Offadesma angasi* (Crosse and Fischer, 1864).

Because details of the natural history of most species of Periplomatidae remain unknown, observations on *Periploma margaritaceum* were undertaken at the Smithsonian Marine Station at Link Port, Ft. Pierce, Florida, in 1982. This is the type species of the genus *Periploma* and serves as a pattern for studies on other species. The information obtained thereby is invaluable in carrying out a planned study on the systematics and zoogeography of the family.

MATERIALS AND METHODS

Collections: Collections of *Periploma* specimens were made in January, April, May, September and November 1982, at low tide (in depths of from 0.5–1.5 m), from grassy sand flats, near St. Lucie Inlet, Martin County, Florida (ca. 27°, 10′N; 80°, 11′W). Salinities varied from 25 to 35‰ depending on tidal flow [the locality is near the mouth of the St. Lucie River]. Method of collection was digging with a shovel to a depth of 15–20 cm, and sieving the substratum with a 0.5 mm nylon screen. Specimens captured were placed in sea water and returned to the laboratory for study. There they were maintained in aerated sea water at ambient temperatures (ca. 27°C) for a week or more while observations were made.

An attempt was made to utilize the mineral, cryolite, as a transparent substratum for observation of the animals *in situ*. While cryolite is an acceptable substratum for such active burrowers as *Mulinia lateralis*, it was not successful for *P. margaritaceum*, probably because its crystals were not ground fine enough. *Periploma margaritaceum* appears to prefer a substratum of fine, silty sand that will pass through a 202 µm screen.

Specimens were observed with a Wild Stereomicroscope in fingerbowls both with and without substratum. If placed on substratum they were allowed to lie on top for a period of time. Since usually no burrowing occurred with the specimens in that position, anterior ends of the clams were gently pushed into the substratum so that they were oriented in presumed natural beginning burrowing position (see Stanley, 1970, p. 99). Burrowing activities were usually initiated within a few minutes following the latter reorientation.

OBSERVATIONS

Habitat: *Periploma margaritaceum,* in the Indian River, Florida, inhabits grassy sand bars near St. Lucie Inlet. It lives buried in silty sand of a particle size less than 202 µm and at depths probably less than a few cm. They have been found in this habitat throughout the year.

Size-frequency: specimens were never abundant during the several occasions I searched for them at St. Lucie Inlet. A summary of the living specimens collected and their length measurements is given in Table 1. No individuals were found at that locality, living or dead, exceeding 10.2 mm in length, although only about 140 km north, at Cocoa Beach, Florida, specimens have been found reaching 14 mm (USNM 608799, 778145), and along the Gulf of Mexico coast, a length of over 30 mm may be reached (USNM 607127). Although specimens from the St. Lucie Inlet population are small in size, gonadal sections indicate they are sexually mature hermaphrodites, the sexual condition typical of anomalodesmatans according to Morton (1981a,b), and Boss (1982). One of the specimens collected in April 1982 contained large numbers of mature ova.

Measurements and statistics shown in Table 1 give a general indication of population changes over the year. Mean length appears to be greatest in May, when optimum temperatures for spawning may be reached. Recruitment of smaller individuals was noted in September and general increase in mean length seems to occur in late November. The mean width/length ratio of 32 specimens collected in November was 0.61.

Anatomical notes: gross anatomy of *P. margaritaceum* is similar to that of *Offadesma angasi* (Morton, 1981b). A small fourth pallial aperture is located just ventral to the incurrent siphon. The mantle is fused from that point to the small pedal opening located anteriorly.

Habits: when placed in a dish of clean seawater, without substratum, the valves of *P. margaritaceum* either remain closed or there may be protrusion of the translucent, spade-shaped foot which probes the bottom of the dish in an attempt to burrow (see Plate 1, Fig. B).

Individuals refuse to burrow in a substratum composed of particles larger than 202 µm or unfamiliar consistency (cryolite, see Materials and Methods). This is probably due to the fact that it causes damage or "discomfort" while passing through the mantle cavity and siphons during burrowing (see below). When placed in a dish of seawater that also contains several centimeters of the silty sand substratum, the foot is protruded and the animal may attempt to bury itself. If it is not successful, and the anterior end is then mechanically introduced into the substratum at a 45° angle, burrowing usually commences and the animal may be completely buried within a few minutes.

The burrowing sequence is as follows: individuals penetrate at an angle by introducing the foot into the substratum and gain a purchase with its enlarged, spade-shaped end. The shell is subsequently pulled down in shallow increments. Specimens removed from the substratum at this time have the mantle cavity packed with silty sand substratum. When the posterior end of the clam's shell is approximately level with the surface of the substratum, and the mantle cavity is packed with sand, burrowing ceases momentarly and the excurrent and incurrent siphons are protruded slowly. The globular excurrent siphon is larger in diameter than the incurrent siphon and bears from 6–9 tentacles surrounding its elongate opening. The incurrent siphon is considerably smaller in diameter and more elongate. Its opening also is surrounded by tentacles. I believe that the tentacles of *Periploma* serve a tactile sensory function, as no eyes have been observed as were found in

Table 1. Comparison of length measurements of live collected *Periploma margaritaceum* from St. Lucie Inlet, Florida, January–November 1982 (N = number of specimens in sample; Range L mm = Range of lengths of all specimens in sample measured in millimeters; M = Mean = average of all specimens measured/number of specimens in sample; SD = Standard Deviation from the Mean; V = Variance).

	Jan	Apr	May	Sept	Nov	
N	4	22	10	15	19	13
Range L mm	3.0–7.7	3.0–9.6	6.5–9.0	4.5–9.8	4.2–10.2	5.7–8.9
Mean	5.8	6.6	7.8	6.2	6.2	7.2
SD	1.8	1.8	0.8	1.6	1.4	1.1
V	3.4	3.4	0.6	2.6	1.8	1.2

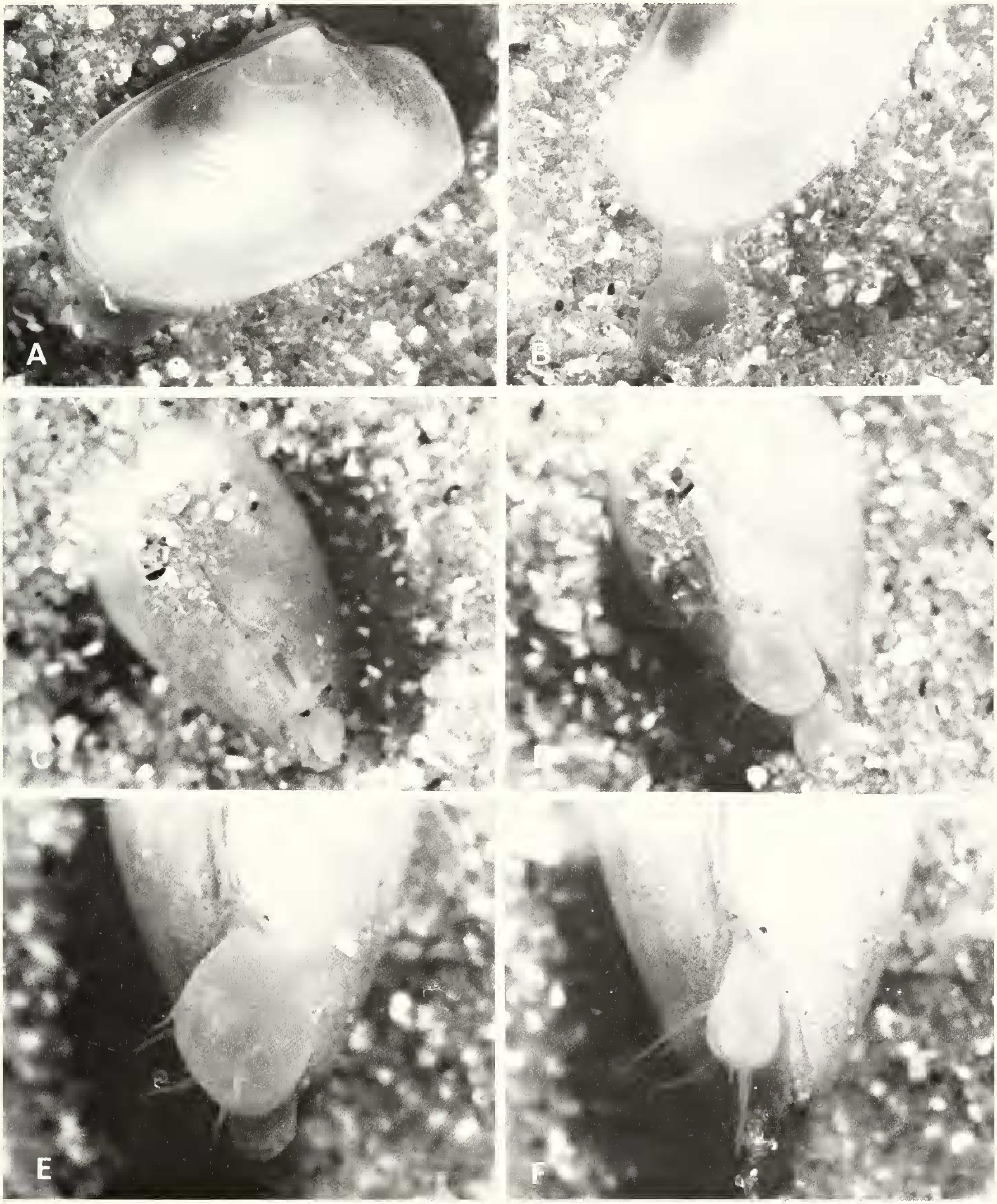

Plate 1. Figs. A–F. Stages in burrowing of *Periploma margaritaceum*, from St. Lucie Inlet, Martin County, Florida, collected April 27, 1982, showing activities of the siphons. A. Individual lying on right valve with foot protruding slightly antero-ventrally from mantle pedal aperture (note intrinsic fracture in uppermost [left] valve at umbo). B. Foot digging into substratum, showing enlarged tip. C. Partially buried, siphons beginning to protrude (note elongate opening of excurrent siphon with 2 tentacles showing). D. Siphons more fully protruded (note contrasting shapes of globular excurrent, and tubular incurrent siphons). E. Excurrent siphon expanded to near maximum; 8 tentacles showing. F. Excurrent siphon contracting (note sand grains being blown out of more ventral incurrent siphon). (Specimen measures 7 mm in length; photos by J. Rosewater).

Laternula by Adal and Morton (1973), nor were they noted in *Offadesma angasi* by Morton (1981b).

Behavior of siphons in cleansing mantle cavity: siphons are initially protruded when the clam is almost completely covered by substratum and only the posterior end of the shell is visible. The excurrent siphon becomes considerably expanded and bulbous; the incurrent siphon also is extended. The opening of the excurrent "bulb" is closed when it has reached maximum size. Next a contraction of the excurrent siphon occurs, followed by a series of contractions of the siphon that expell water and accumulated sand and debris out through the incurrent siphon, clearing the mantle cavity. The animal then resumes burrowing and disappears into the substratum. It then reopens a single "respiratory-feeding" aperture in the sand through which there is periodic expulsion of sand grains via a water current. (see Plate 1, Figs. A–F, depicting the series of burrowing stages).

DISCUSSION

The population of *P. margaritaceum* at St. Lucie Inlet has a mean length that appears small for the species (individuals collected over an 11 month period averaged 6.6 mm in length; see Observations and Table 1). These individuals are reaching sexual maturity, as indicated by gonad sections and examination of specimens having mature ova (April 1982). Available size-frequency data indicate that St. Lucie individuals reach sexual maturity in late spring, with newly settled individuals becoming apparent in November. These data indicate a one year life history. Further data are required before definitive statements can be made regarding the life history of *P. margaritaceum*.

Observations on living periplomatids have been rather rare probably due to their subtidal habitat and cryptic habits. Analyses of habitats have been made on only a few species. Allen (1958) reported *Cochlodesma praetenue* (Pulteney, 1799) to occur in fine gravel, sand and muddy sands from spring low tide line to depths of 60 fathoms, although most commonly the species lives in sand and sandy gravel in sheltered areas just below low water. There individuals are buried to a depth of 7 cm below the surface of the substratum where they lie with one valve down, usually the right one. Harry (1976) found *Periploma orbiculare* Guppy, 1882, to occur in substrata of more than 50% mud/sand in Lower Galveston Bay, Texas. Littleton (1982) analysed distributions of *P. orbiculare* and *P. margaritaceum* in Matagorda Bay, Texas. He found them to be well separated ecologically based on the types of sediments in which each lives: *P. orbiculare* generally inhabited sediments at mid bay composed of from 80 to 100% mud at a range of depths from 1.52 to 3.66 m; *P. margaritaceum* occurred in sediments nearer shore composed usually of greater than 71% sand and at a range of depths from 0.61 to 3.66 m (but usually shallower than the deepest depth cited). Since the shell of *P. orbiculare* is more rounded in outline than that of the rather wedge-shaped *P. margaritaceum*, it appears that there is a correlation between shell shape and habitat: softer sediments allowing clams with a less streamlined-shaped shell to burrow more easly, whereas those with wedge-shaped shells can penetrate a more dense, sandy substratum with greater ease. Morton (1981b) found *Offadesma angasi* in several localities in North Auckland, New Zealand, living in shallow water at a depth of 7–8 cm in firm sand, always lying on its left valve, inclined at an angle of 20°, with both siphons extending to the surface of the substratum. In this study *P. margaritaceum* occurred living in silty sand, probably quite similar to its habitat as previously described by Littleton (1982). It seemed to prefer a particle size of less than 202 μm for burrowing and this substratum was provided for my laboratory observations.

Burrowing activities of bivalves, as summarized by Stanley (1970), generally consists of several stages: beginning with 1. the foot probing downward into the substratum and enlarging at its tip; 2. closing of siphons; 3. forcible adduction of valves with resultant ejection of water from the ventral mantle opening; 4. retraction of the foot which pulls the shell downward into the substratum; 5. relaxation of the adductor muscles allowing the valves to gape; and finally, 6. a resting stage prior to the renewal of the cycle. In many mollusks strong shell adduction ejects a water current out the pedal mantle opening forcing the substratum away from the anterior portion of shell at the same time the foot is pulling the animal downward. This has been observed clearly in such strong burrowers as the surf clam, *Spisula solidissima* (Dillwyn, 1817) (Ropes and Merrill, 1966).

In contrast with the surf clam, periplomatids are sluggish burrowers. Morse (1919) pointed out that *Anatina papyratia* Say [sic] (= *Periploma fragile* Totten, 1835) is very timid and sluggish and performed little while he observed it. He was able to observe that its siphons are separate, and noted that the excurrent siphon was inflated to twice the diameter of the incurrent siphon. Tentacles surround both siphonal openings. Allen's (1958) description of *Cochlodesma praetenue*, a related form, showed similarities and gave more details. That species lives buried, usually on its right side, with the incurrent siphon extending upward toward the surface of the substratum, and the excurrent siphon extended posteriorly (horizontally) into the substratum. Both siphons form mucous lined tubes. Unpublished observations by H. W. Harry (*in litt.*, 1967) show the gross anatomy, mantle and siphon characters of *Periploma orbiculare* Guppy, to be very similar to other periplomatids, except that he could find no ventral opening in the mantle. *Thracia pubescens* (Thraciidae) has been reported by Forbes and Hanley (1853, pp. 219–238), and Yonge (1937), to have similar appearing siphons to those of Periplomatids, except that both siphons of *Thracia* extend to the surface of the substratum, and two siphonal holes are found at the ends of the substantial mucous-lined tubes. It was suggested by Forbes and Hanley (1853) that the siphons of *Thracia* are used to eject "water and 'rejectamenta' with greater force" [from the mantle cavity]. The latter was questioned by Yonge (1937) who believed the peculiar appearing siphons fit them only for tube formation. Morton (1981b) reported that *Offadesma angasi* is unable to reburrow once it is removed from its substratum. He noted peristaltic waves from base to tip of its siphons, possibly an indication the species is capable of some of the activities observed in the siphons of *P. margaritaceum.* The siphonal anatomy of most periplomatids described to date appears grossly similar to that of the siphons of *Periploma margaritaceum* which help that clam burrow and clear its mantle cavity through muscular, bellows-like contractions. The extensive mantle fusion noted in this species, and the anteriorly located small pedal aperture, undoubtedly contribute to its ability to close off and flush the mantle cavity. The function of the fourth pallial aperture is not known. It possibly may serve as a 'relief valve' when the mantle is under internal pressure during contraction of the excurrent siphonal bellows (see Observations).

Valves of both Thraciidae and Periplomatidae are very fragile, and subject to breakage. This is common to Pandoracea in general (Taylor, Kennedy and Hall, 1973, p. 282, table 20). As suggested by Prezant (1981) there are correlations evident between shell structure, habitat and the evolution of bivalves. Morton (1981b) recommended separate superfamily status for Periplomatidae, Laternulidae and Thraciidae: Thraciacea Stoliczka, 1870, based on similarities in their shells and ligaments. Shells of Periplomatidae are buttressed internally to the intrinsic crack in their valves at the umbos, but it is doubtful they could survive the repeated adductions performed by other bivalves in burrowing and in ejecting pseudofaeces and other foreign matter from the mantle cavity.

Adal and Morton (1973) and Morton (1973, 1976) have analysed the functional anatomy of Laternulidae, a family often considered to be close in relationship to Periplomatidae. Greatest similarities appear to be related to the presence of intrinsic fractures at the umbos of both valves, buttressing of the fractures with shelly material on the inner surfaces of the valves, the shape of the chondrophore and the possession of a lithodesma. Some very basic differences between the two families are that the siphons of Laternulidae are joined and non-retractable, while in Periplomatidae they are separate and retractable; siphonal eyes were reported in *Laternula* by Adal and Morton (1973), but have not yet been observed in periplomatids; there is a permanent posterior shell gape in Laternulidae, but the posterior shell closes tightly in Periplomatidae; laternulids are oriented vertically in the substratum, while periplomatids are oriented horizontally.

On the basis of his analysis of the shells of Laternulidae, Morton (1976) proposed that the vertical umbonal fractures permit the shell to be adducted like four partly disjointed functional valves, allowing the shell to close and mantle-siphonal currents to be generated. My observations on *P. margaritaceum* and other periplomatids indicate a very basic difference from Laternulids in the function of the siphons and generation of these currents.

I suggest that the described siphonal activities of periplomatids replace the muscular adduction used in such forms as *Spisula.* The current generated by the bellows-like excurrent siphon of *Periploma margaritaceum* flushes the mantle cavity of sand and debris that enters the pedal mantle opening during foot probing/burrowing activities, and by the same means helps remove substratum from the clam's path. A forceful anteroventrally directed current, such as the one that helps bivalves like *Spisula* displace the substratum and excavate their burrows, is not needed in *Periploma.* The fragile valves of *Periploma* are thus preserved from being fractured further and burrowing is achieved. Since only one siphonal opening penetrates the substratum following burrowing, it is presumed that *P. margaritaceum,* like *Cochlodesma praetenue* [observed by Allen (1958)], extends only its incurrent siphon toward the substratum surface, while its excurrent siphon extends horizontally and continues to perform periodic bellows-like actions to cleanse the mantle cavity during further burrow excavations. Additional observations of these activities utilizing a transparent substratum are planned to verify these interpretations.

The bellows-like activities of *Periploma* siphons function both in burrowing and cleansing of the mantle cavity of the "rejectamenta" referred to by Forbes and Hanley (1853), which would include pseudofaeces. This siphonal activity, in which water is passed retrograde to the ordinary respiratory-feeding current, into the mantle cavity via the excurrent siphon and carries sand and debris out the incurrent siphon, is readily seen in other bivalves when pseudofaeces are expelled.

The fact that these siphonal activities have not been observed in periplomatid species other than *P. margaritaceum* is surprising since most species studied have similar siphonal anatomies (Pelseneer, 1911; Morse, 1919; Allen, 1958; Harry, *in litt.*; Morton, 1981b). It is quite possible that younger individuals are most active insuring more rapid establishment of settling populations. Older individuals may become more sluggish, but *P. margaritaceum,* at least, will reburrow and perform siphonal activities readily if encouraged by partially imbedding anterior ends in suitable substratum. These siphonal activities may be interpreted as an adapation to life in a soft sandy-mud substratum.

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